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Water temperature as an indicator of environmental variability on a coral reef

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Abstract

The magnitude and spatial extent of variation in water temperatures commonly experienced by corals were examined on several temporal scales to evaluate the association between environmental stability and habitat favorability. Shallow reef-top sites were exposed to surface waters modified by prevailing weather conditions; the deeper outer slopes lay permanently within a well buffered, relatively oceanic water mass. Thermal stability and relative water movement were poor predictors of coral growth and survival. The most stable and the most unstable thermal environments were both poor habitats for corals.

The view that tropical reefs are extremely stable, predictable, and benign physical environments for living organisms, on both short ecological and long evolutionary time scales (e.g. Wells 1957; Newell 1971; Grassle 1973), has been modified by growing awareness of spatial and temporal heterogeneity, not only among different reefs, but also within a single reef (Connell 1978). It has long been recognized that different parts of a reef may differ substantially in their favorability for coral survivorship and growth (e.g. Mayer 1918; Wells 1952; Loya 1972; Glynn 1976). However, the less favorable (and often more variable) habitats are frequently ignored during reef studies or are regarded as atypical "extremes" (e.g. Wells 1957), although Glynn (1973, 1976) and Connell (1978), in particular, have recognized the importance of spatial variation in physical and biological processes affecting the ecology of corals. Descriptions of physical variation on reefs tend to concentrate on relatively rare, often catastrophic, events of short duration, such as extremely low tides (Glynn 1968; Loya 1972), freshwater runoff (Cooper 1966), or hurricanes (Rogers et al. 1982). The implication remains that generally stable and benign conditions prevail between these periodic disturbances, although few data have been published to document this assumption. Discussions of temperature, for example, often emphasize lethal or sublethal extremes (e.g. Mayer 1918; Vaughan 1918; Hudson 1981), while saying much less about variation on a day-to-day basis.

Our primary purpose is to indicate the magnitudes and the spatial and temporal scales of everyday physical variation experienced by corals living in several habitats on a single reef. Although Heron Island had been a center of reef research for over 20 years when we started to work there, data suitable for making similar comparisons were not available from that or any other reef. During repeated visits from 1974 to 1981, we accumulated data on water temperatures within a few centimeters of living corals. Temperature is not necessarily the most important variable affecting an organism, or even always a relevant one, but it is the most easily measured physical factor and one that is often used alone to characterize

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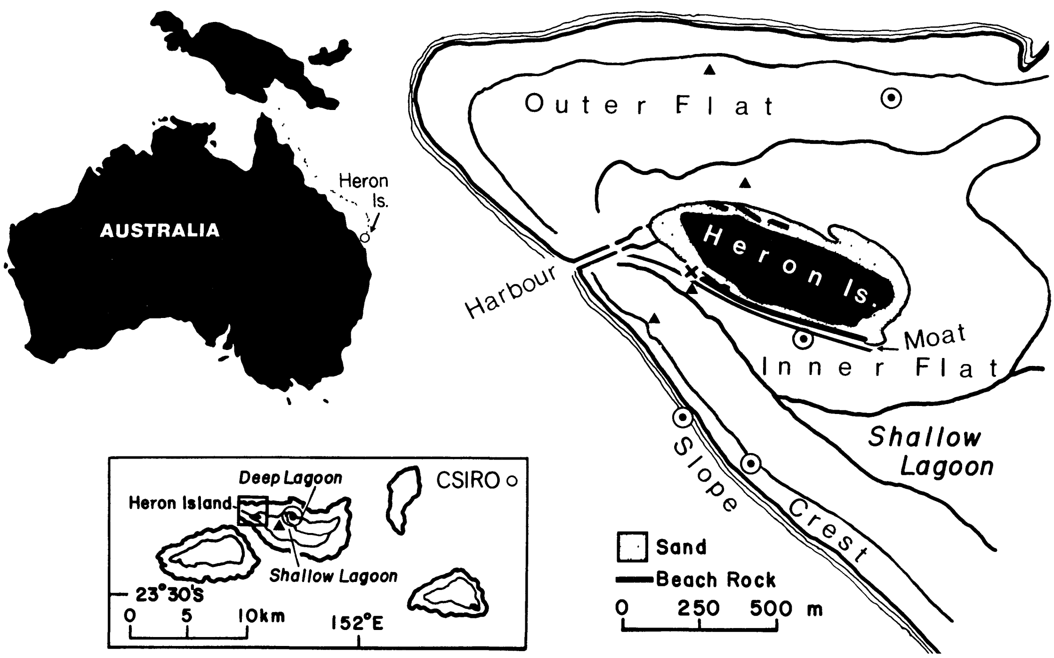

Fig. 1. Western part of Heron reef showing major habitats. Data collecting stations: main sites—⊙; moat temperature station—×; additional temperature or relative water movement stations—▲; CSIRO oceanic station—O.

environmental conditions. We summarize here both average temperatures and some aspects of typical temporal and spatial variation on tidal, daily, and seasonal scales in five major habitats occupied by corals. Although we included some relatively unfavorable habitats, we saw no signs of extensive mortality attributable to thermal extremes. We also include limited data on relative water movement, partly as a factor likely to affect temperature locally, but chiefly because it provides another index of environmental variation.

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Field area

Locality—Heron Island (23°26′S, 151°55′E) lies near the western end of the second largest emergent reef of the Capricorn-Bunker group, at the southern end of the Great Barrier Reef (Fig. 1). The Heron reef is about 9 × 4 km, with an area of about 27 km² (Jell and Flood 1978). It is a lagoonal platform reef with steep outer walls 15–20 m high and an almost flat upper surface, much of which is occupied by a shallow lagoon with <1 m of water at low tide. A deeper lagoon, occupying about 20% of the reefal area, has an average depth of about 3.5 m at low water. The shallow inner flat is separated from the island by a slightly deeper moat, 10–50 m wide and up to 50 cm deep at low tide. Maxwell et al. (1964) and Jell and Flood (1978) give detailed descriptions of the reef.

For much of the year (February/March–September) the prevailing winds are the southeast trades, averaging 5–11 $m \cdot s^{-1}$ (Jell and Flood 1978). In summer (October–February) the tradewinds continue, often with a northeasterly component (Pickard et al. 1977), but they may be interrupted by extended periods of calms, or light northwesterly winds, or by occasional hurricane force winds associated with tropical cyclones (Brandon 1973; Jell and Flood 1978). Tidal amplitude ranges from 2.8 m on extreme spring tides to about 0.8 m on extreme neap tides (Jell and Flood 1978). There is a general flow of water to the southwest (Woodhead 1970), but major currents are tidal, reversing direction every 6 h. Current patterns and velocities around the reef are greatly modified by prevailing winds, but rarely exceed 0.56 $m \cdot s^{-1}$ (Jell and Flood 1978). Maxwell et al. (1964) reported a maximum current velocity of 1.3 $m \cdot s^{-1}$.

Sites—Data were recorded from several sites, most within 0.5 km of the island. The five main sites were being used for long term, experimental demographic studies of the abundant, widely distributed and ecologically important *Acropora palifera/Acropora cuneata* group of corals (Potts 1976, 1977, 1978, 1984). These habitats span much of the range of physical and biological conditions experienced by corals on the Heron reef and the experimental sites were chosen as particularly well developed representatives of each habitat (Potts 1978). The inner flat site (25 m from the beach with 10–20 cm of water at low tide) marked the shoreward limit of coral growth. The outer flat site (50–100 cm deep at low tide) was protected by the crest from heavy wave action. The crest site on the outer margin of the reef was exposed to the air at low tide and to continual heavy wave action from prevailing winds and storms. The slope site was at the bottom of the reef (in about 15 m of water) where continuous coral cover gives way to a sand and rubble bottom. The lagoon site was in the deeper lagoon, 2.5 km east of the island, where it was furthest removed from oceanic influences but close to the "tidal watershed" of minimal horizontal water movement (Maxwell et al. 1964). Other sites on the flats and in the shallow lagoon (*see Fig. 1*) were used for studies of skeletal chemistry (Swart 1979, 1980*a,b,* 1981; Swart and Coleman 1980; Swart et al. 1983) and for short term monitoring of particular environmental factors. Potts (1978, 1984) and Swart (1980*a*) give more extensive descriptions of the sites.

Methods

Temperature—All water temperatures were recorded on maximum-minimum thermometers (±0.5°C) calibrated at 20°C against a standard thermometer. Continuous records were kept in the moat near the southwest end of the island from 27 March 1976 to 17 June 1977. The thermometer was shaded from direct sunlight by a large boulder and remained submerged in 5–10 cm of water on even the lowest tide. From August 1974 to November 1976, thermometers were placed at the five main sites and read whenever the sites were visited. For short periods in November 1975 and November 1976, they were read every 24 h. Unpublished oceanic data for a permanent station (23°25'S, 152°07'E) east of Heron Island were made available by R. J. Edwards.

Relative water movement—Weight loss from uniform "clods" (about 4 × 3 × 3 cm) of calcium sulfate was used as an index of relative water movement (Doty 1971). The clods were cast in ice-cube trays and their bases sandpapered to 25 g of dry weight. All clods used were cast on the same day by a standardized mixing procedure. Their order of use was randomized. Each clod was glued to a Plexiglas plate (about 10 × 3.5 cm). In the field, plates were anchored with twists of wire and exposed for 24 h. Before and after exposure, clods and plates were weighed after equilibration to atmospheric humidity. Doty's (1971) discussion suggested that weight loss should be linearly related to the total volume of water passing in close proximity to the surface of the clod. Sets of five replicate clods were exposed at two reef-flat sites on 5 days in January and February 1978, and sets of three replicates were exposed at four reef-flat sites on four consecutive days in March 1981 (Fig. 1). Agreement among replicates was good, after we discarded those that were damaged, e.g. by fishes [avg mean wt loss = 10.03 ± 0.56 g (SE); $n = 26$ sets, 3–5 clods per set]. Single clods were exposed at the five main sites on three consecutive days in November 1975 and six consecutive days in November 1976.

Results

Seasonal variation—By using maximum-minimum thermometers, we recorded all extreme temperatures occurring at any hour of the day and any state of the tide or weath-

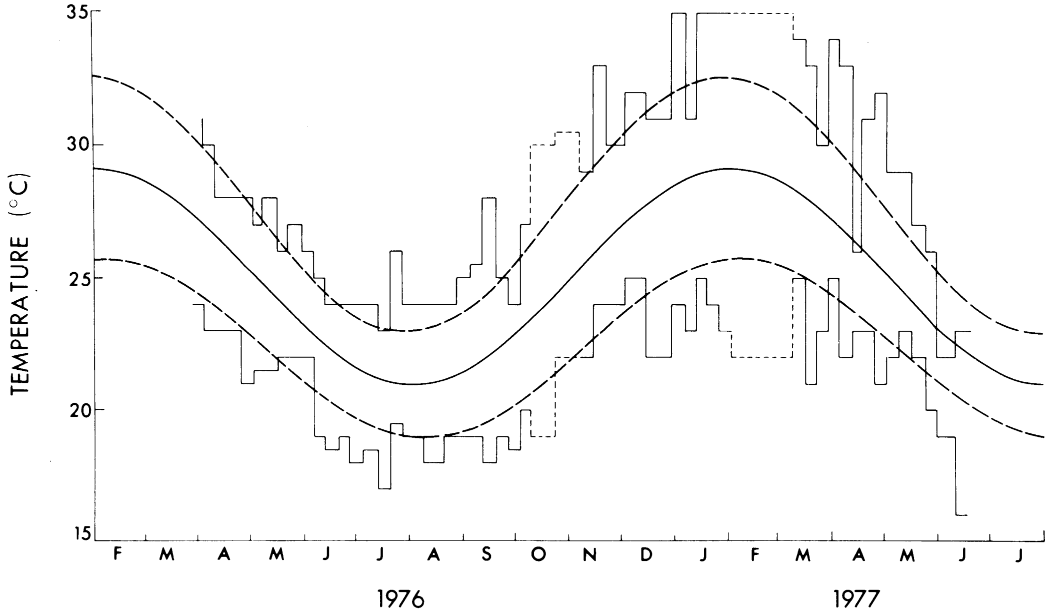

Fig. 2. Weekly (5–9-day intervals) maximum and minimum water temperatures in the moat. Dashed sections indicate three longer periods of 14, 14, and 35 days. Curves indicate predicted daily mean (solid) and maximum and minimum (dashed) temperatures.

er conditions. Since 75% of our observations from the moat cover intervals of 48 h or less, these data form the most detailed continuous record from Heron Island and the longest published series (15 months) from a shallow reef-top habitat on any reef (Fig. 2). The data were analyzed using GLIM, a general linear modeling package (Baker and Nelder 1978) to fit sine curves by least-squares regression. The general form of the equation (expressed in radians) is

$$T = M - a \cdot \sin\left[\frac{2\pi \cdot (j - K)}{365}\right]$$

where T is predicted temprature (°C), M is mean annual temperature, a is half the amplitude, j is day of year (1–365), and K is a constant locating the horizontal position of the curve.

Weekly maximum and minimum temperatures from the moat, plus predicted curves for daily maximum, minimum, and mean temperatures are shown in Fig. 2, while Table 1 contains details of the equations. The mean annual temperature of 25.04°C was higher than the 23.9°C cited by Weber and Woodhead (1972). Good agreement between observed and predicted values (r^2 = 0.75–0.84) and inspection of residuals both indicated regular sinusoidal progressions of temperature throughout the year. Predicted maximum temperature was highest on 28 January and lowest on 29 July; predicted minimum lagged by 10 days, highest on 7 February and lowest on 8 August.

Previously reported temperatures from Heron Island came either from the inner flat (Endean et al. 1956; Frank 1969), or from oceanic stations away from the reef (Brandon 1973; CSIRO unpubl. data). Only

Table 1. Parameters and explained variation of regression equations describing curves (in Fig. 2) of predicted daily water temperatures for the moat.

	Mean	a	K	r^2
Max	27.79	−4.835	119	0.78
Min	22.28	−3.356	129	0.75
Mean	25.04	−4.078	123	0.84

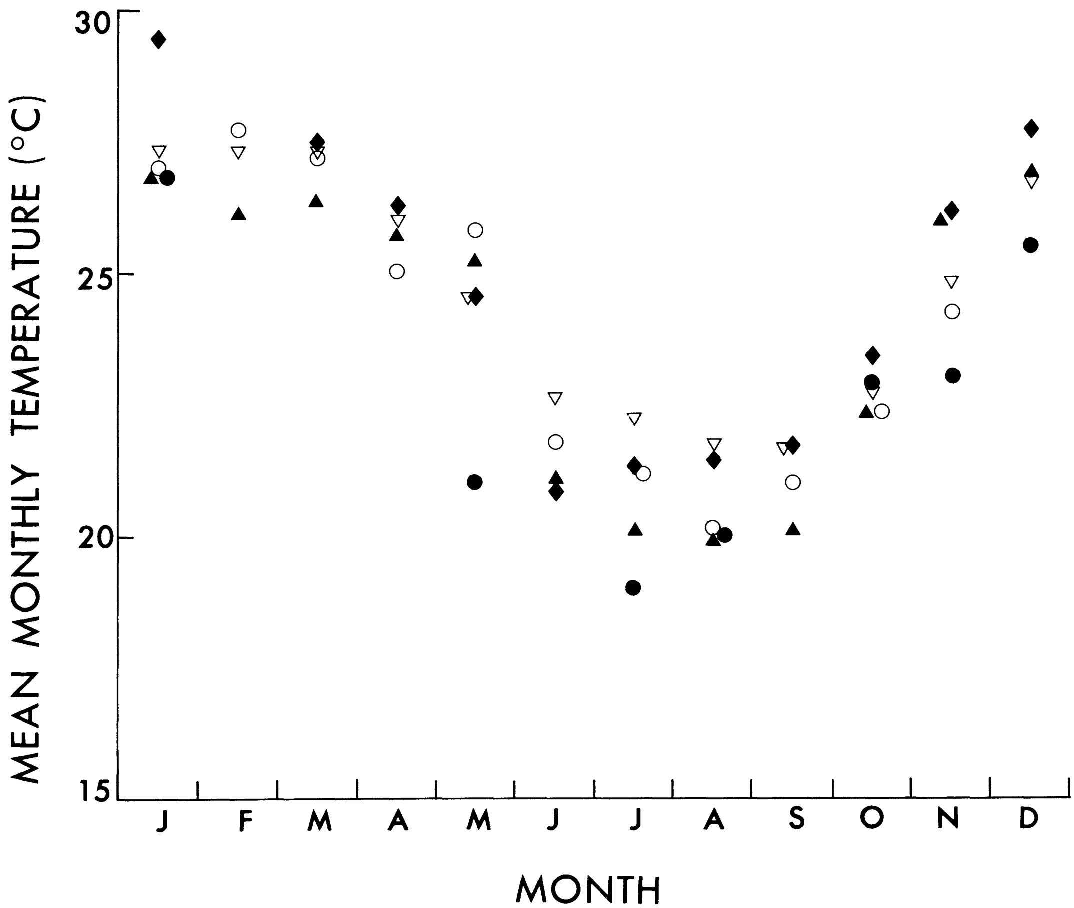

Fig. 3. Mean monthly water temperatures reported from Heron Island. Inner flat (solid symbols): 1954–1955 (●—Endean et al. 1956); 1967—1968 (▲—Frank 1969); 1976—1977 (◆—this paper). Oceanic (open symbols): dates unknown (○—Brandon 1973); 1977–1978 (▽—CSIRO unpubl.).

Frank's data came from maximum-minimum thermometers; the others were gathered in various ways, but all seem to be instantaneous readings. Most of these data were expressed as monthly means and they are summarized in Fig. 3, which also contains our data from the moat expressed in the same way. Although daily maximum and minimum temperatures in the moat tended to be 0.5°–1°C less extreme than those taken about 400 m away at the main inner flat site, our mean moat temperatures were so similar to those on the inner flat that they can be compared directly with the data of Endean et al. and Frank. Table 2 contains details of sine curves fitted to each set of monthly data, grouped into inner flat and oceanic sites.

Mean monthly oceanic and inner flat temperatures were very similar, the chief difference being a 2-week lag at oceanic sites in the dates of predicted highest and lowest temperatures (Table 2). Average monthly temperatures are relatively predictable from year to year, since the range of means on the flat never exceeded 5°C for any month, and in 8 months was <2°C (Fig. 3). On the inner flat, predicted mean annual temperature and annual range in 1976–1977 were greater by 2.2°C and 1.4°C than in 1954–1955; values for 1967–1968 were intermediate (Table 2).

Table 2. Parameters and explained variation of regression equations predicting mean monthly water temperatures.

	Mean	a	K	r^2	Date of Max	Date of Min	Source
Inner flat							
1954–1955	22.68	−3.491	112	0.95	21 Jan	22 Jul	Endean et al. 1956
1967–1968	23.83	−3.756	127	0.89	5 Feb	6 Aug	Frank 1969
1976–1977	24.90	−4.207	121	0.97	30 Jan	31 Jul	This paper
Mean flat	24.00	−3.877	124	0.86	2 Feb	3 Aug	
Ocean							
?	24.10	−3.489	138	0.95	16 Feb	17 Aug	Brandon 1973
1977–1978	24.54	−3.108	134	0.98	12 Feb	13 Aug	CSIRO unpubl.
Mean ocean	24.33	−3.306	136	0.95	14 Feb	15 Aug	

Extreme temperatures—During 1976–1977, observed mean monthly temperatures in the moat varied by about 8.6°C, from 20.8°C in June to 29.4°C in January. This is the largest annual range reported from Heron Island (Table 2). It is 2°C more than the mean oceanic annual range and 3.6°C more than the 5°C maximum range reported by Weber and Woodhead (1970). However, 1976–1977 temperatures from the moat and nearby flat were much more variable, ranging from 16° to 35°C. Even more extreme temperatures were recorded by the maximum-minimum thermometers left untended for long periods at the main sites. The lowest temperature we recorded was 13.5°C, on the inner flat in August 1974 and on the outer flat in winter 1976. The highest temperatures recorded were 36°C in the lagoon in February and 37°C on the inner flat in March 1975.

Daily variation—Since mean temperature ranges of maximum-minimum thermometers read at intervals of 24 and 48 h were not significantly different, all records from 1- and 2-day observation periods were pooled to give between 5 and 27 records for each month (Fig. 4). Mean daily ranges were all between 3° and 5°C for most of the year (March–November), but they increased to almost 9°C in January. The monthly variances of daily temperature ranges were relatively small in winter and summer, but increased substantially during periods of rapid temperature change in autumn (March–May) and spring (September–November).

The largest daily temperature range recorded in a 24-h period was 12°C in the moat on 18–19 March 1977. This probably is close to the maximum daily range likely to occur anywhere on the Heron reef, because the site is very close to the island and exposed to the vagaries of local weather conditions for long periods at low tide. It was only 1°C less than the maximum monthly range of 13°C, also in March 1977, and only 2°C less than the 14°C maximum monthly range observed in 1954–1955 by Endean et al. (1956).

Tidal variation—On 49 dates from 24 November 1977 to 15 January 1978 and from 16 March to 15 April 1981, instan-

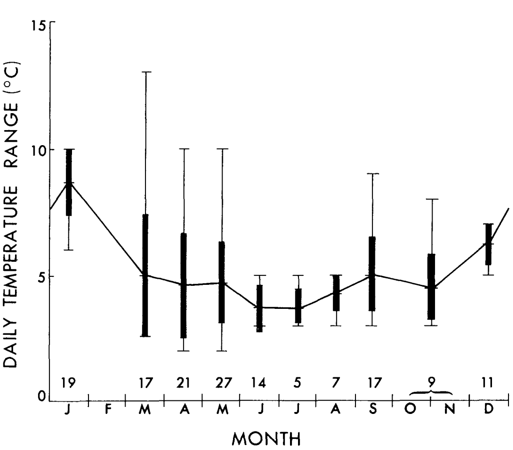

Fig. 4. Monthly means, standard deviations, and ranges of daily ranges of water temperature in the moat, using all records for 1- and 2-day periods. Numbers of observations in each month are shown.

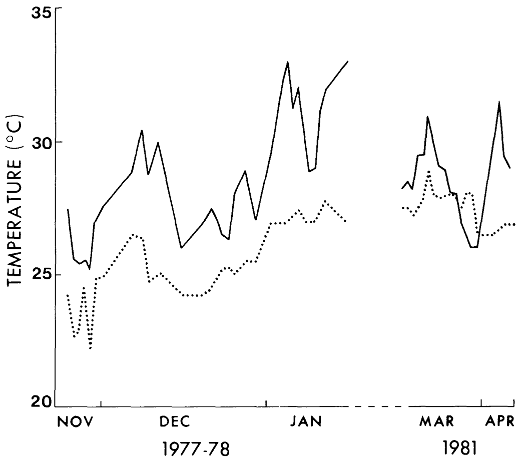

Fig. 5. Instantaneous daytime water temperatures on the southern outer flat at low tide (solid line) and high tide (dotted line) on the same dates.

taneous water temperatures were taken during the day at high and low tide on the outer flat south of the island (Fig. 5). Temperatures at high tide (about 23°–28°C) were always similar to mean oceanic temperatures in those months (Fig. 3). Excluding 6 days of storms (25–30 March 1981), temperatures at low tide were up to 6°C higher than high water temperatures on the same day. The mean difference was 2.72° ± 1.57°C (SD). Differences were correlated positively with time of low water (and hence cumulative insolation) and negatively with wind speed (and hence evaporative cooling) (Swart 1980*a*). Only during rainy weather was water temperature at high tide either similar to or greater than that at low tide. Maximum daily temperatures on the flats appear closely associated with weather conditions during daytime low tides; presumably, minimum water temperatures are associated with exposure during nocturnal low tides.

Spatial variation—From August 1974 to November 1976, maximum-minimum thermometers were read every few weeks at most of the five main sites. Comparable records are not available for all sites and dates because breakages were frequent, and no attempt was made to keep permanent thermometers on the wave-exposed crest. Average temperatures and ranges (max-min) are listed in Table 3. Average temperatures usually differed <2°C among the sites except in summer when the warmest site, the inner flat, tended to be 3°–4°C warmer than the coolest site, usually the slope. However, rankings of the sites by average temperature for the six time intervals with complete data

Table 3. Average temperatures/ranges (°C) during corresponding periods at the five main sites from August 1974 to November 1976.

		Site				
	Days	Inner flat	Lagoon	Outer flat	Crest	Slope
Aug 74	8	19.3/11.5	18.5/5.0	19.8/8.5		21.3/1.5
Aug–Sep 74	14	21.0/11.0	19.0/4.0	20.3/7.5		21.3/1.5
Sep 74	14	21.3/10.0	20.0/4.0	21.5/8.5		20.3/1.5
Sep–Oct 74	14	21.0/10.0	20.5/5.0	21.5/9.0		21.5/2.0
Oct–Nov 74	48		22.5/7.0	23.5/13.0		23.0/4.0
Dec 74–Jan 75	57	26.5/19.0	24.5/8.0			24.8/2.5
Jan–Mar 75	54	29.5/15.0	29.0/14.0			25.5/3.0
Mar–Apr 75	23		25.8/5.5	23.8/6.5		25.0/4.0
Apr–May 75	26		25.0/6.0	24.5/6.0		24.0/3.0
May 75	14		23.3/2.5	24.8/4.5		22.8/0.5
May–Jun 75	36		20.5/7.0			21.5/1.0
Nov 75	3	26.0/8.0	25.3/5.5	26.0/6.0	25.8/5.5	25.3/2.0
Mar–Aug 76	150	24.3/19.5	22.8/13.0	21.8/16.5		
Nov 76	6	28.3/8.5	29.3/8.5	28.0/7.0	29.0/9.0	26.3/2.5
Ranges						
Mean ±1 SD		12.67±4.24	6.79±3.27	8.45±3.47	7.25±2.47	2.23±1.07
(Mean rank)*		(1.08)	(2.75)	(2.17)		(4.0)

* Six complete data sets (excluding crest site); ranges are significantly different by Kendall's coefficient of concordance ($W = 0.886$; $P < 0.001$).

Table 4. ANOVA of temperature ranges among sites (excluding crest) from Table 3 (ns—not significant, $P > 0.05$).

Source	SS	df	MS	F	P
Complete data sets					
Sites	223.75	3	74.58	45.55	<0.001
Residual	32.75	20	1.64		
Total	256.5	23			

A posteriori comparisons

Inner $\overset{*}{>}$ Outer $\overset{*}{>}$ Lagoon $\overset{\dagger}{>}$ Slope

Source	SS	df	MS	F	P
All data					
Sites	608.6	3	202.87	20.90	<0.001
Residual	417.4	43	9.71		
Total	1,026.0	46			

A posteriori comparisons

Inner $\overset{*}{>}$ Outer $\overset{\text{ns}}{>}$ Lagoon $\overset{\dagger}{>}$ Slope

* Significant at $P < 0.05$.
† Significant at $P < 0.001$.

(excluding the crest) were not significant (Kendall's coefficient of concordance $W = 0.236$, $P > 0.05$).

Although average temperatures were similar at all sites during corresponding periods, the variation in temperature differed markedly among sites. For the six time intervals with complete data, rankings of the sites by temperature range were highly significant (Kendall's coefficient of concordance $W = 0.886$, $P < 0.001$). In addition, inspection of Table 3 shows that within the eight time intervals with incomplete data, the ranks of available sites are consistent, in every case, with the mean rankings of the complete data sets.

Temperature ranges among sites were analyzed further, using GLIM, in a 1-way ANOVA followed by comparisons of individual cells (Table 4). The effects of site were highly significant and explained 87% of the variation in the six complete data sets; even when the incomplete data sets were included, almost 60% of the variation was explained. The inner flat had the most variable temperatures ($P < 0.05$). Temperature variation was intermediate on the outer flat and lagoon; the lagoon was usually less variable than the outer flat. The most stable site was always the slope ($P < 0.001$), where ranges rarely exceeded 3°C, even during periods when those at other sites reached 19°C. We did not have enough data from the crest to assess its relative variability, but it appeared similar to the nearby outer flat.

Relative water movement—Because $CaSO_4$ clods mounted on the substrate measure water movements actually experienced by benthic organisms at the water–substrate interface, these clods provide a simple, economical way to integrate all sources of water movement (currents, tides, winds, local turbulence) into a single measure of relative water movement. Weight losses from uniform clods exposed for 24-h periods in 2 years at the five main sites are summarized in Fig. 6. They were exposed under a range of wind and tidal conditions. The data were analyzed, using GLIM, in a 2-way ANOVA (year × site) with three covariates: mean wind speed, estimated from readings at 0900 and 1500 hours (Bureau of Meteorology monthly summaries for Heron Island); maximum amplitude of a single tidal cycle; and the sum of all vertical tidal displacements during the 24-h period. The last two were estimated from tide tables (Department of Harbours and Marine 1975, 1976).

All three covariates and both factors were significant and together they explained 89% of the variation (Table 5). The three covariates explained 26% of the sums of squares, with mean wind strength explaining more than half the variation attributable to co-

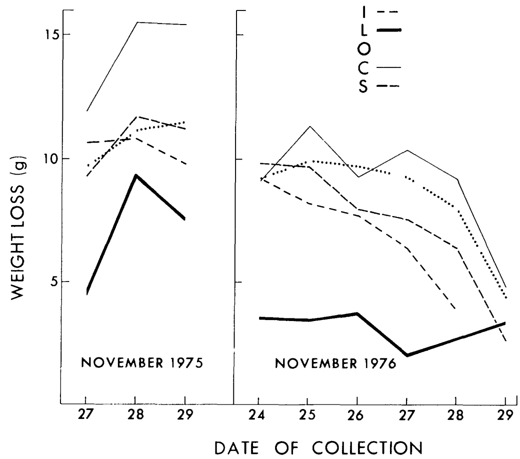

Fig. 6. Weight loss from 25-g $CaSO_4$ clods at the five main sites during 24-h periods from 26–29 November 1975 and 23–29 November 1976. Sites: inner flat—I; lagoon—L; outer flat—O; crest—C; slope—S.

variates. The significant effect of year probably reflects curing of the $CaSO_4$ clods, which were only a few weeks old in November 1975. A year later their solubility was significantly lower, even after adjusting for effects of the covariates. The interaction between year and site was not significant and site remained the single largest source of variation ($r^2 = 0.43$). A posteriori comparisons showed that relative water movement was much greater on the crest than in the intermediate sites (outer flat, slope, inner flat; $P < 0.001$), while water movement in the protected deep lagoon was much less than at any of the other sites ($P < 0.001$).

Discussion

Pickard et al. (1977) noted that most physical data reported from the Great Barrier Reef and Coral Sea covered very limited timespans, and that much of the variation present in the original data was concealed because most data were published as monthly or annual means or ranges. They identified only one extensive series of daily and weekly environmental records: the simple physical and chemical measurements taken in several habitats by the Great Barrier Reef Expedition to the Low Isles in 1928–1929 (Orr 1933*a,b*; Moorhouse 1933; Orr and Moorhouse 1933). Half a century later, these records remain among the most comprehensive published data on environmental variation from reefs in any part of the world.

Table 5. ANOVA and explained variation of weight loss from $CaSO_4$ clods at the five main sites (ns—not significant, $P > 0.05$).

Source	SS	df	MS	F	P	r^2
Covariates						
Wind	62.4	1	62.4	40.5	<0.001	0.14
Max tide	36.4	1	36.4	23.6	<0.001	0.08
Sum tide	14.2	1	14.2	9.2	<0.01	0.03
Sum covariates	113.0	3	37.7	24.5	<0.001	0.26
Factors						
Year	78.6	1	78.6	51.0	<0.001	0.18
Site	187.2	4	46.8	30.4	<0.001	0.43
Year × site	9.2	4	2.3	1.5	ns	0.02
Explained SS	388.0	12	32.3	21.0	<0.001	0.89
Residual	46.2	30	1.5			
Total	434.2	42				

A posteriori comparisons

Crest $\overset{*}{>}$ Outer $\overset{\text{ns}}{>}$ Slope $\overset{\text{ns}}{>}$ Inner $\overset{*}{>}$ Lagoon

Outer $\overset{\dagger}{>}$ Inner

* Significant at $P < 0.001$
† Significant at $P < 0.01$.

A few sets of extended temperature records are available from reefs, but they concentrate on seasonal and year-to-year variation and give limited information about small-scale spatial and temporal patterns. Except for the data of Glynn (1973), all seem to have been taken at relatively oceanic stations unlikely to reflect temperatures in shallow reef-top habitats (Seckel and Yong 1977; Crossland 1981; Walker 1981). Most were reported as monthly means (plus variances or ranges), usually based on periodic (often weekly), instantaneous readings. Hourly bathythermograph records (Schroeder 1977; Hudson 1981) are available only from deeper slope and interreef stations (2.5–15 m). Our data on temporal and spatial variation illustrate how misleading it can be to characterize the physical properties of an entire reef in a few summary statistics or to assume they are representative of conditions experienced by organisms in all habitats.

Our data on temperature and relative water movement suggest that at least two water masses affect the Heron reef: a shallow surface mass over the reef top that is greatly influenced by prevailing weather conditions, and a more oceanic water mass largely restricted to the outer slopes. The large ranges in water temperature on the crest were similar to those at the other shallow sites (Table 3), indicating that the crest was exposed to reef-flat or lagoonal water moving off the reef. Conversely, the very small ranges measured barely 100 m away in 15 m of water suggest that the slope site was exposed permanently to oceanic water; the extreme temperature range on the slope from 1974 to 1976 was only 19.5°–27.5°C (Table 3), which is very similar to the mean annual oceanic range (Fig. 3). The two water masses were often separated by shallow thermoclines (<5 m) or by vertical shear zones accompanied by differences in turbidity or temperature that were readily detectable by swimmers. While oceanic waters may reach the reef top by surging up grooves in the reef front (Roberts et al. 1977), the thermal stability at 15 m suggests that there is little or no downward movement of surface water. The differences between low and high tide temperatures on the outer flat (Fig. 5) suggest that some shallow habitats, including the crest, are exposed to both water masses: oceanic at high tide and reef-flat or lagoonal water at low tide.

Isolation of reef-top surface water from the surrounding oceanic waters by shear zones and thermal discontinuities appears to be common on reefs (Boden 1952; Hamner and Hauri 1977, 1981). The weekly, monthly and seasonal variations in water temperature at 15 m on the outer slope of Grand Bahama Island (26°30′N) are very similar to those at our slope site, and they too give no indication of thermal influences from nearby reef-flats (Schroeder 1977). It seems probable that the physical stability associated with oceanic water masses will prevail over most parts of the reef only on narrow fringing reefs that lack raised margins to impound surface waters (e.g. Curacao: Bak and Luckhurst 1980).

Usual thermal conditions on the Heron reef consist of complex patterns of tidal, daily, lunar, and seasonal variation, with marked spatial heterogeneity among habitats. Other physical and chemical factors have not been monitored extensively on Heron Island, but short term studies of oxygen tension (Kinsey and Kinsey 1967), cations (Davies 1974), and stable isotopes (Weber and Woodhead 1971; Swart 1980*a*; Swart and Coleman 1980; Swart et al. 1983) indicate analogous temporal and spatial scales of variation. Individual organisms, even those in apparently similar habitats but on different parts of the reef, may experience different water masses, temperature regimes, water movements, exposure at low tide, and variation in other physical and chemical properties. Moreover, these properties can change abruptly in only a few meters. For example, while organisms on the crest and at the foot of the slope may be less than 50 m apart, they appear to spend much of their time in different water masses with different temperature regimes.

Patterns at Heron Island are probably quite representative of many other reef systems, even though Heron (23°26′S) lies close to the southern limit of reefs. Vigorous hermatypic corals and reefs exist in higher latitudes and in coastal waters where extremes of temperature, salinity, and turbidity are greater (Kinsman 1964; Macintyre and Pilkey 1969; Veron 1974; Crossland 1981; Grigg 1981). Even in low latitudes, small-scale temporal and spatial thermal variation is likely to be marked on any reef with extensive shallow habitats heated by insolation during the day and cooled by evaporation and radiation at night. Both the differences between oceanic and reef-flat temperatures and the patterns of daily variation in shallow habitats that we observed at Heron Island are similar to those in analogous habitats at Low Isles (16°30′S: Orr 1933*a,b*; Moorhouse 1933; Orr and Moorhouse 1933) and Palau (7°30′N: Motoda 1940). At Arno Atoll (7°N), mean oceanic temperature was 28° ± 1°C all year round, but instantaneous daytime temperatures on the inner flat ranged from 27°C to 36.5°C within a month (Wells 1952). Similarly, Mayer (1918) noted a 12.5°C range over 24 days at Maer Island (10°S), also based on instantaneous daytime readings. In every case, use of maximum-minimum thermometers probably would have increased the observed ranges by recording both nocturnal and diurnal extremes.

Pronounced spatial variation in physical conditions implies that all parts of the reef are not equally benign. When genetically similar arrays of corals of the *A. palifera*/*A. cuneata* group were introduced to the main experimental sites (Potts 1978, 1984), growth and survivorship in each habitat differed markedly (Table 6). Neither thermal stability nor relative water movement is a good indicator of coral growth and survival in the different habitats, nor is one index of environmental stability a good predictor of the other. Relative growth is a particularly good index of everyday favorability, because it reflects long term, cumulative, physiological responses to more favorable environmental conditions. Conversely, mortality is an index that assesses responses chiefly to the most unfavorable conditions. By both criteria, the protected outer flat, with intermediate levels of environmental stability, was the most favorable site for corals. The slope and inner flat were both extremely unfavorable habitats, but for very different reasons. Although the slope had the most stable temperature regime on all scales from diurnal to seasonal, it was also the least benign environment where high mortality and slow growth rates probably reflected chronic exposure to low light intensities (which reduce photosynthesis by symbiotic algae) and continual heavy silting. At the other extreme, the unfavorable inner flat had the most unstable thermal environment on all temporal scales measured, and this is probably also true of other factors, such as salinity (Swart and Coleman 1980) and oxygen tension (Kinsey and Kinsey 1967). While environmental instability may explain continual high mortality rates on the inner flat, slow growth probably reflects restriction of growth to frequent, short periods (probably daily) of favorable conditions, rather than being caused by chronically unsuitable conditions (Potts 1978, 1984). These conclusions suggest that simple indices of environmental conditions must be applied cautiously when making comparisons within and between reefs.

Table 6. A. Environmental stability among the main sites assessed by two indices, mean temperature range (from Table 3) and relative water movement (from adjusted means of clod weight loss, Table 5). B. Environmental favorability for corals assessed by two indices, relative survivorship and growth in experimental populations of *A. palifera*/*A. cuneata* from November 1974 to August 1977 (from Potts 1984). Indices are expressed as proportions of values for the least stable and most favorable sites.

	Inner flat	Lagoon	Outer flat	Crest	Slope
A. Stability					
Temp range	1.00	0.54	0.67	0.57	0.18
Water movement	0.77	0.51	0.88	1.00	0.83
B. Favorability					
Survival	0.34	0.69	1.00	0.89	0.15
Growth	0.54	0.59	1.00	0.63	0.19

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